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Long-term effects of deer browsing: Composition, structure and productivity in a northeastern Minnesota old-growth forest

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ABSTRACT

Although the immediate impacts of elevated deer (*Odocoileus* spp.) browsing on forest regeneration have been well documented, few studies have examined the longer term consequences. A deer exclosure experiment was initiated in 1991 in an old-growth northern mixed mesic forest in northeastern Minnesota, and resampled in 2008 to examine changes in composition, structure and productivity. Decades of overbrowsing by white-tailed deer have led to almost complete recruitment failure in size classes >2.5 cm dbh for preferred deer browse species *Thuja occidentalis* and *Pinus strobus* in unprotected plots. Other palatable browse species have been severely limited in understory development (*Populus tremuloides*, *Betula papyrifera*, *Fraxinus nigra*). Within exclosures, *P. strobus* gained in all size classes <20 cm dbh, while *F. nigra*, *B. papyrifera*, *T. occidentalis* all showed significant gains. Non-preferred *Picea glauca* increased outside exclosures, but has also gained within exclosures. The increase in *P. glauca* across treatments indicates a long-term legacy effect of preferential browsing. Browsing induced suppression of subcanopy density of preferred species and failure of canopy tree replacement may lead to a more open woodland structure dominated by *P. glauca*. Browsing pressure may negatively impact productivity, as whole tree biomass in exclosures increased at a rate twice that of unprotected plots. The low biomass levels recorded in 2008 (unprotected: 98.0 mg/ha^{-1}, exclosure: 104 mg/ha^{-1}) are approximately 1/2 of values typically recorded in later successional forests in this region indicating lower productivity may be another longer-term legacy of elevated deer population. Continued high browsing pressure is one of many factors contributing to the restructuring of northern Great Lakes forests away from historical variability conditions towards a novel and more homogeneous forested landscape. These simplified forests may be less resilient to the suite of emerging stressors such as climate change and less able to provide ecosystem services such as carbon storage, biological diversity and forest products. Sustained restoration efforts, along with reductions in deer density will be needed to restore species and structural diversity.

1. Introduction

Ungulate browsers influence composition, structure and ecosystem processes in north-temperate forests by selectively foraging on preferred plant species (Pastor et al., 1993). Moose (*Alces alces*) at high densities alter vegetation biomass, productivity, composition, nutrient cycling and litterfall (McInnes et al., 1992), and also influence the spatial patterns of vegetation patches (Pastor et al., 1998). Rising deer populations (*Odocoileus* spp.) in many regions of North America now exert a pervasive influence on forest ecosystem dynamics. These include understory plant species diversity (Alverson et al., 1988; Stockton et al., 2005), understory and overstory woody vegetation composition and structure (Whitney, 1984; Horseley et al., 2003), forest songbirds (McShea and Rappole, 2000; Allombert et al., 2005a) and forest invertebrates (Allombert et al., 2005b).

Decades of high white-tailed deer (*Odocoileus virginianus*) populations in the northern Great Lakes region may contribute to a large-scale restructuring of forested communities in this region (Rooney and Waller, 2003). Extensive logging and large, slash-fueled fires of the European settlement period created a more homogeneous forested landscape across the northern Great Lakes region where dominance shifted from later successional or mid-seral conifer and hardwood species to early successional hardwood species (Friedman and Reich, 2005; Schulte et al., 2007). The subsequent shift to even-aged timber harvest as the primary disturbance factor perpetuated this compositional shift and also imposed a new spatial pattern dominated by small forest patches (White and Host, 2008). The predominance of small patches created high edge density and low interior forest space (Wolter and White, 2002), that along with early-successional forest favors

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species such as white-tailed deer, but negatively impacts edge-sensitive forest birds (Temple and Flaspohler, 1998) and tree regeneration due to herbivory (Alverson et al., 1988). Thus, white-tailed deer are one of a suite of related factors including land-use history, economics (timber markets and the forest products industry), development, exotic-invasive species and climate change that will have long-lasting impacts on the composition, structure and function of northern Great Lakes forests. Elevated populations of white-tailed deer in the northern Lake States region have led to limited regeneration success for many preferred browse species such as eastern hemlock (*Tsuga Canadensis* [L.] Carr), northern white cedar (*Thuja occidentalis* L.), eastern white pine (*Pinus strobus* L.) and northern red oak (*Quercus rubra* L.) (Anderson and Loucks, 1979; Cornett et al., 2000; Anderson et al., 2002; Rooney and Waller, 2003). Many herbaceous species are also prone to browsing damage as they never grow out of the zone of susceptibility (Rooney and Waller, 2003).

Although there is strong documentation of the impacts of deer browsing on tree regeneration, there is little information about the longer term impacts on sapling, subcanopy and canopy layers in mature and old-growth northern Great Lakes forests. Ross et al. (1970) analyzed vegetation within and outside of one exclosure in a north-central Minnesota pine forest from 1946 to 1969. They determined that browsing suppressed growth of all preferred browse species, with only non-preferred species moving into the subcanopy. Zenner and Peck (2009) compared the same exclosure (Ross et al., 1970) to plots with no treatment, and recent repeated underburning. Only the exclosure contained sufficient mid-story density of white pine to maintain a pine canopy. The untreated plot will likely succeed to northern hardwoods. White pine regeneration was highest in the burned plot, but was restricted to the seedling layer do to deer browse and shrub competition. Salk et al. (2011) found that prolonged deer browse in an old-growth hemlock-hardwood forest in northern Michigan led to recruitment failure of preferred browse species (white cedar, eastern hemlock, yellow birch) leading to a long-term shift in dominance towards less preferred sugar maple.

Recent work shows that prolonged, intensive browse leads to top-down effects (extremely simplified understory vegetation) that have bottom up impacts on the food chain as understory invertebrate and shrub-dependent songbird communities also became more simplified (Martin et al., 2010). Evidence suggests that prolonged, intense browsing pressure may lead to profound change in forest composition and structure leading to altered food chains (Martin et al., 2010), declines in regional habitat and species diversity and changes in key processes such as nitrogen and carbon cycling (Rooney and Waller, 2003; Côté et al., 2004).

Exclosure studies have important limitations; varying and unknown deer densities, lack of replication (Horseley et al., 2003), and that fact that complete protection from browsing is an artificial condition, as they do not capture the background levels of herbivory that would occur under low ungulate density levels. However, they can still provide valuable insights into the role of herbivores in structuring plant communities and how ecosystems may recover when browsing is eliminated or reduced. Specifically, exclosure studies help us understand the potential for ecosystem recovery after being subjected to elevated deer browsing. This includes data on the length of time that browsing protection is necessary to ensure adequate regeneration. Exclosure studies may also indicate that other management actions in addition to browse protection may be needed; gap creation, thinning or brush control to release regeneration or actions such as prescribed fire or scarification to create favorable seed bed conditions.

At a site in northern Minnesota, the following questions were explored: (1) how did selective browsing on preferred tree species by white-tailed deer influence composition, structure and productivity in unfenced compared to fenced plots over a 17 year period? (2) Did pre-fencing browsing create a legacy effect on composition and productivity?

The forest dynamics observed in this study are broadly applicable to mesic conifer-hardwood forests with elevated deer populations throughout the region. Although this study was conducted at a single site in northern Minnesota, the soils, glacial landforms, climate conditions and plant communities are representative of mesic forests within the North Shore Highlands subsection (MN Dept. Nat. Res., 1999) and more generally of mesic forests of the Lake Superior Basin. While impacts on tree regeneration and understory vegetation are well documented (Rooney and Waller, 2003), much less is known about how these impacts influence the complete stand age structure beyond the understory. This study presents one of the few longer-term data sets available for examining the impacts of herbivores on the full range of stand age structure.

1.1. Study area

The study area comprises 4200 ha located in the North Shore Highlands subsection of the Minnesota Ecological Classification System (MN Dept. Nat. Res., 1999) and includes a remnant 182 ha stand of old-growth eastern white pine and northern white cedar forest known as Cathedral Grove. Ten kilometers of the Lake Superior shoreline form the southern boundary of the study area. Proximity to Lake Superior influences local climate conditions, creating cool, moist conditions in spring and summer and warmer conditions in fall and winter relative to inland areas (Baker and Keuhnast, 1978; Baker et al., 1985). Part of the Nemadji–Duluth Lacustrine Plain, soils are typically deep, moderate to well-drained clays with shallow, rocky, well-drained soils on the ridges (Minnesota Soil Atlas, 1973). This area is part of a large white-tailed deer wintering yard paralleling Lake Superior from Duluth to Canada.

The study area consists of a complex mosaic of forest and wetland communities. The matrix upland forest is composed of northern mesic mixed forest, which includes varying mixtures of quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.) and balsam fir (*Abies balsamea* [L.] Mill), white spruce (*Picea glauca* [Moench] Voss), white pine and white cedar) (MN Dept. Nat. Res., 2003). Prior to European settlement (~1900) and the extensive logging of that period, high severity fires occurred at a rotation of approximately 220 years (MN Dept. Nat. Res., 2003). Catastrophic windthrow was uncommon in the North Shore Highlands, with a rotation period in the range of 3000 years (White and Host, 2008). Currently, the Cathedral Grove forests are in a late-successional growth stage where tree fall gaps created by tree mortality and small (1–3 tree) windthrow events are the primary canopy disturbances influencing tree growth and regeneration.

In the pre-European settlement period, upland forests in the North Shore Highlands subsection were dominated by mixtures of eastern white pine, eastern white cedar, white spruce, balsam fir, paper birch and quaking aspen. Northern hardwood patches composed of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula allegheniensis* Britt.) and northern white cedar occurred on loamy uplands within the boreal conifer–hardwood matrix (White and Host, 2000). White pine (9–19% to 0.2–1.0%) and white cedar (6–11% to 3.2–4.2%) have both declined precipitously from the pre-European settlement period to present in the North Shore Highlands subsection (White, 2001).

Prior to European settlement, northeastern Minnesota's severe winters and mixed-conifer and hardwood forests were poor habitat for white-tailed deer, which occurred at very low densities or may have been absent from the area prior to the early 1900s (Nelson and Mech, 1981). The post-Euro-American settlement shift to